

# A spatial model to estimate gear efficiency and animal density from depletion experiments

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**Abstract:** Depletion experiments are conducted to estimate efficiency of sampling gear and density of organisms. Traditional models for analyzing these experiments make restrictive assumptions that are often violated. We present a new spatial model, suitable for sessile benthic invertebrates, that does not depend on these restrictive assumptions. The new model (i) allows flexibility during the experiment in choosing the spatial location of successive samples, (ii) does not require organisms or successive samples to be randomized over the entire area of the experiment, and (iii) permits target organisms to be lost or added during the experiment. The model treats total catch per sample as a sum of catches from smaller cells with different, but known, sampling histories. A negative binomial model is used to describe the distribution of catches from tows made during the depletion experiment. Maximum likelihood methods are used to estimate parameters, derive confidence regions for parameters, and evaluate goodness of fit between data and the model. Data from an experiment involving Atlantic surfclams (*Spisula solidissima*) are used to demonstrate the model.

**Résumé :** Des expériences d'épuisement nous permettent d'estimer l'efficacité des engins d'échantillonnage et la densité des organismes. Les modèles couramment utilisés pour analyser ces expériences font des présuppositions restrictives qui sont souvent violées. Nous présentons une nouvelle modélisation spatiale applicable aux invertébrés benthiques sessiles qui ne dépend pas de ces présuppositions restrictives. Le nouveau modèle (i) permet une flexibilité durant l'expérience pour choisir le site des échantillonnages successifs, (ii) ne requiert pas que les organismes ni les échantillons successifs soient répartis au hasard sur toute la surface expérimentale et (iii) permet que des organismes ciblés soient perdus ou ajoutés au cours de l'expérience. Le modèle traite la capture totale par échantillon comme la somme des captures de cellules plus petites avec des histoires d'échantillonnage différentes, mais connues. Un modèle binomial négatif sert à décrire la distribution des captures provenant des traits de récolte durant l'expérience d'épuisement. Des méthodes de vraisemblance maximale permettent d'estimer les paramètres, de déterminer les intervalles de confiance de ces paramètres et d'évaluer l'ajustement entre les données et le modèle. Des données provenant d'une expérience avec les mactres de l'Atlantique (*Spisula solidissima*) nous servent à faire la démonstration du modèle.

[Traduit par la Rédaction]

## Introduction

A central problem in fisheries science is estimation of the catchability coefficient, a scalar that converts measures of relative abundance to absolute estimates of abundance. One can estimate the catchability coefficient of sampling gear by carrying out a depletion experiment, in which samples are taken without replacement from a closed population and catch per unit of sampling effort is monitored. Depletion experiments (e.g., Lasta and Iribarne 1997) are needed when it is not feasible to sample organisms directly with box cores, grab samples, or in situ sampling by divers. Direct sampling with divers may be too risky or impractical. Even when direct sampling is feasible, it may not be possible to sample a sufficient number of organisms or to cover a large enough area of the bottom (e.g., Caddy 1968; Smolowitz and Nulk 1982). Additionally, direct sampling methods can have cer-

tain biases related to the scale of observation or selectivity of the gear for limited size ranges.

The first depletion models for closed populations were developed by Leslie and Davis (1939) and DeLury (1947). Those early models included the following primary assumptions: (i) all extant individuals have the same probability of being caught in a sample, (ii) the expected catch in a sample is proportional to sampling effort, (iii) the catch depends on the cumulative catch of preceding samples, and (iv) all removals are known. In sampling a population of sessile organisms with a dredge, these assumptions are violated in subtle but important ways. A dredge sample can be viewed as the summation of a set of quadrats linked by the tow path. Because of an inability to accurately control the tow path of a dredge in deep water, one cannot assume that the probability of sampling a particular quadrat is random. The length of the tow and the number of previous tows through each

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quadrat determine the number of animals caught in a particular tow. In a traditional experiment, one expects the number of animals per tow to decline monotonically with the number of tows. For sessile animals being sampled with a dredge, the catch in later tows may increase depending on the location of the tow. Another source of variation arises when availability of organisms changes during an experiment (e.g., Kendall and Bjorkland 2001; Peterson et al. 2004). Thus the variation in catches can exceed that expected under a standard depletion model that assumes a multinomial distribution for catches from a closed, nonspatially distributed population (Gould and Pollock 1997). The excess variation (i.e., overdispersion, sensu McCullagh and Nelder 1989) is not all due to the spatial distribution of animals, but also arises from the sampling process itself. This is related to the problem of heterogeneous capture probabilities described in Pollock et al. (1984) and Hilborn and Walters (1992).

Several models have been developed to address cases in which one or more of the traditional depletion model assumptions are violated (Carle and Strub 1978; Chien and Condrey 1985; Wang and Loneragan 1996). Mohn and Elner (1987) demonstrated that when the population is not uniformly distributed, the Leslie–Davis model underestimates abundance and overestimates gear efficiency. Miller and Mohn's (1993) analysis of sources of bias in depletion experiments demonstrates the need to consider spatial heterogeneity of organisms. Joll and Penn (1990) explicitly addressed the spatial aspect of sampling in their analyses of scallop (*Amusium balloti*) and western king prawn (*Penaeus latisulcatus*) populations.

Beginning with Taylor (1953) and continuing to Power and Moser (1999), various investigators have characterized the empirical distributions of catches of aquatic animals using a negative binomial distribution  $\sim \text{NB}(\mu, k)$ . We also employed this distribution in our model. The applicability of the NB model can be demonstrated theoretically as the summation of a Poisson random process with randomly varying capture probabilities (see Johnson et al. (1993) and references therein), as well as empirically (Houser and Dunn 1967; Welch and Ishida 1993; White and Bennetts 1996). The NB model explicitly accounts for the extra variation in observed catches and reduces to the Poisson distribution as the dispersion parameter  $K$  becomes large.

Two additional properties of the NB distribution make it appropriate for the analysis of catches in a depletion experiment. First, the catch in a tow is the sum of catches from individual patches, each with the number of organisms distributed as NB random variables. The sum of individual random variables drawn from a NB distribution with parameters  $\mu$  and  $k_i$  is also distributed as a NB random variable with parameters  $\mu$  and  $\sum k_i$  (Johnson et al. 1993). Second, the dispersion parameter  $K$  is invariant with respect to changes in density, which would occur as a result of removals (Pielou 1977, p. 128).

Overdispersion of count data has been demonstrated in many applications of the Leslie–Davis and DeLury removal models (e.g., Paloheimo 1963; Otis et al. 1978; Schnute 1983). Both parametric (e.g., Wang and Loneragan 1996) and semiparametric (e.g., Gould and Pollock 1997) methods for dealing with overdispersion have been applied to deple-

tion experiments. Following the rationale of Lawless (1987), who emphasized the utility of relating the overdispersion to the underlying processes, we chose the NB model as a parametric approach to describe overdispersion. Our application of the NB model uses the cumulative spatial pattern of animal removals to define the probabilities of capture and expected catch per tow. This approach is tailored to sessile organisms sampled by a device the position of which is difficult to control. The likelihood function for the NB in our model explicitly conditions the parameters in each successive probability density function of the likelihood function on the cumulative spatial pattern of removals.

Our new model has been used to estimate dredge efficiency in National Marine Fisheries Service (NMFS) research surveys of the Atlantic surfclam, *Spisula solidissima* (Northeast Fisheries Science Center (NEFSC) 2003), ocean quahog, *Arctica islandica* (NEFSC 2004), and sea scallop, *Placopecten magellanicus* (NEFSC 2001). In the model, animals are distributed across the sea floor in a matrix of square cells. The catch in a single sample (i.e., tow) represents the sum of catches from all cells (under the constraint that cell width  $\geq$  the width of the sampling device) that were contacted. The total catch depends not only on the number of cells sampled, but also on the sampling history of each cell in the tow path. A NB model is used to describe the distribution of catches, and maximum likelihood methods are used to estimate parameters, derive confidence regions, and evaluate goodness of fit. Parameters that are estimated include initial (presampling) density of animals, efficiency of sampling gear, indirect effects of sampling gear on catches (such as the burial of clams by a clam dredge), and the clumping parameter of the NB model. To demonstrate the model, we applied it to data from a field experiment on clams.

## Existing theory

The expected catch  $E(C)$  in a sample from a closed population can be expressed as the product of population abundance ( $N$ ), sampling effort ( $f$ ), and efficiency ( $e$ ) of the sampling device. If we assume that  $f$  is equal to the area swept by the gear ( $a$ ) divided by the total area ( $A$ ) of the closed population, then expected catch can be expressed as

$$(1) \quad E(C) = e(a/A)N$$

where  $e$  is the probability of capture given encounter with the fishing gear, and  $a/A$  is the probability of encounter. If the animals are randomly (i.e., Poisson) distributed within the potential sampling area before each sample is taken, then the probability of encounter will be proportional to the area sampled by the gear,  $a$ , divided by the total area of the experiment,  $A$ . Likewise, if the animals are randomly distributed as groups, with varying numbers of individuals, then the probability of encountering a group will still be proportional to  $a/A$  but the expected variance of  $C$  will be higher (Sampson 1988).

The Leslie and Davis (1939), DeLury (1947), and Ricker (1975) models for depletion experiment data begin with the premise that the catch is equal to the probability of capture  $\times$  population size in a fixed area at the start of the interval. Average density following a removal is equal to initial population size minus the catch, all divided by the total area. Every

time sampling takes place, all individuals are assumed to have the same probability of being captured. The Leslie–Davis model is obtained by recursively applying eq. 1, which gives the population size after each catch. Writing the terms  $e(a/A)$  in eq. 1 as  $q$  and recursively applying eq. 1 results in the Leslie–Davis equation:

$$(2) \quad E(C_i) = q(N_0 - T_{i-1})$$

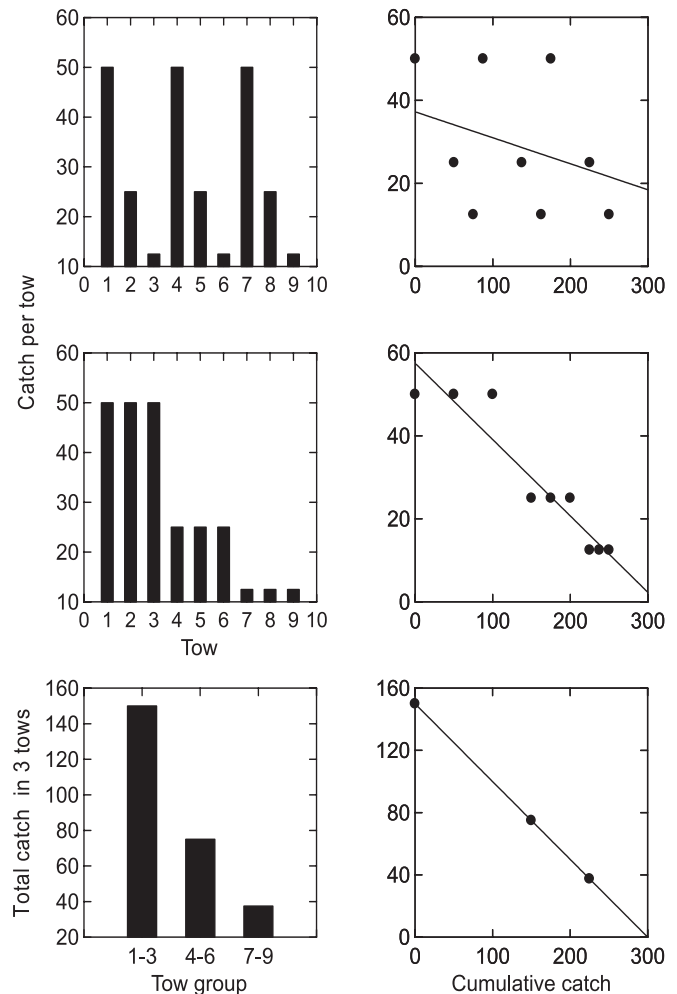
where  $T_{i-1} = \sum_{j=1}^{i-1} C_j$  for tow number  $i$ . Thus the expected catch in the  $i$ th sample  $E(C_i)$  is proportional to the initial population size minus the cumulative catch from previous samples ( $T_{i-1}$ ). Although eq. 2 can be written as a linear regression, a least squares method is not appropriate in this case because the variance of  $C_i$  changes with each observation (Seber 1973; Schnute 1983). Gould and Pollock (1997) showed that maximum likelihood estimation (MLE) was the most appropriate method for estimating the parameters of the Leslie–Davis model.

### Need for spatial approach

Existing theory models catches from a closed population without considering the organism's spatial distribution or the location where the sample was taken. For sessile animals, a removal experiment may be more properly viewed as sampling from a collection of cells in a grid, each of which may be subject to sequential sampling. The expected value of catch in any single sample depends on which cells were sampled and the number of times that each was sampled previously.

The following example demonstrates how failure to consider the spatial pattern and temporal sequence of catches in a depletion experiment can dramatically bias the estimates of true underlying population size and gear efficiency. Consider an experiment with sessile organisms in which the experimental area is wider than the width of the sampling device (Fig. 1). Assume that the experimental area is three paths wide, true population size is 300 individuals, gear efficiency is 0.5, a total of nine tows are taken, and each of the paths is sampled three times. We consider three hypothetical scenarios in which the paths are swept in different orders. In scenario 1, the first three tows are taken in the same path, the second three tows occur in the next path, and the last three tows occur in the remaining path. Naïve application of maximum likelihood methods to the scenario 1 data results in a very low and biased estimate of efficiency (0.06) along with an incorrect high estimated population size (~595). In scenario 2, each of the first three tows occurs in a different path, with no overlap between them. The same occurs for the next three tows (numbers 4–6) and again for the last three tows (numbers 7–9). MLE-based estimates for scenario 2 were also biased, with an efficiency estimate of 0.18 and population estimate of 312. One could recover the true parameters from either scenario 1 or scenario 2 by appropriately summing the tows related to the first, second, and third passes within a path. To show this, we derive scenario 3 from scenario 2 by summing tows 1 to 3, 4 to 6, and 7 to 9. Estimates of efficiency and population size for scenario 3 were equal to their true values, 0.5 and 300, respectively. The idealized experiments described above would be much

**Fig. 1.** Three hypothetical depletion experiments demonstrating that parameter estimates will be biased unless spatial information on sample location is incorporated.



more complicated if tows had partial overlap with each other, as they would in a field experiment.

### Extending the model to allow partially overlapping paths

Failure to consider the spatial pattern of samples biases parameter estimates. Partial overlap of tows, due to inability to control the exact tow path, results in observed catches that are a function of the numbers removed on previous tows and the locations of previous removals. A starting place for modeling this complex situation is to model catch data from depletion experiments in terms of average density in the experimental area, rather than total population size  $N$ . Population size, a parameter in the Leslie–Davis model, is less useful as an abundance index in this case because the size of the experimental area  $A$  is arbitrary, depending on the set of realized tow paths. Average density, however, is a useful measure of abundance because it does not rely on the particular set of tow paths.

Reparameterization of the Leslie–Davis model in terms of average density rather than population number can be shown for a restricted case in which the area swept by a single tow

$a$  and the experimental area  $A$  are constant. The average density is  $D = N/A$ , so that  $A = N/D$ . Substituting for  $A$  in eq. 1 gives  $C = eaD$ . The average density in the cell after removal of  $C$  animals is  $(N - C)/A = N/A - C/A = D - (eaD)/A = D(1 - (ea/A))$ . Recursive computation of catch, population size, density, and cumulative catch is summarized for three time steps (Table 1). The elemental equation derived in Table 1 demonstrates that the expected catch in a cell that has been swept  $j$  times is

$$(3) \quad E(C_j) = eaD_0(1 - e(a/A))^{j-1}$$

Equation 3 expresses catch per sample as a function of animal density, but further development of the model is needed to handle the case in which the probability of capture for animals inside the tow path is  $e$  and the probability for animals outside the tow path is zero. To address this issue, we treat a tow path as a string of individual cells, each of which is characterized with the same nonzero sampling probability. Cells that are not sampled by that tow are not included, in contrast with an analysis that considered all animals in the entire experimental area as equally vulnerable.

To implement this concept, it is necessary to define a "hits" matrix that represents the path of a tow as a discrete string of adjacent cells and retains a record of the number of previous contacts of these cells by the sampling device. The expected value of catch from an individual cell along a tow path can be predicted using eq. 3. The expected catch for the entire tow can now be represented as the sum of the expected catches from all cells. In effect, each cell within a tow can be viewed as an individual depletion experiment. Because the catch in the  $i$ th tow is the sum of catches from individual cells, it is the sum of catches from cells hit 1 to  $i$  times. Thus the expected catch for a tow depends not only on the path of the sampling device, but also on the sampling history of each cell (Fig. 2). Equation 3 can be modified to account for hits of cells:

$$(4) \quad E(C_i) = ea_i D_0 \sum_{j=1}^i f_{i,j} (1 - e\gamma)^{j-1}$$

where  $C_i$  is the number caught in tow  $i$  ( $i = 1, \dots, I$ ),  $e$  is the efficiency, i.e.,  $\text{Prob}(\text{capture}|\text{encounter})$ ,  $a_i$  is the area swept by tow  $i$ ,  $D_0$  is the initial density (number/area), and  $f_{i,j}$  is the fraction of tow  $i$  that was hit  $j$  times, where  $\sum_{j=1}^i f_{i,j} = 1$ .

The parameter  $\gamma$  is analogous to the  $a/A$  term in eq. 3 and is defined as the ratio of the width of the sampling device  $w_{\text{dredge}}$  to the width of the cell  $\Delta x$ :

$$(5) \quad \gamma = w_{\text{dredge}} / \Delta x$$

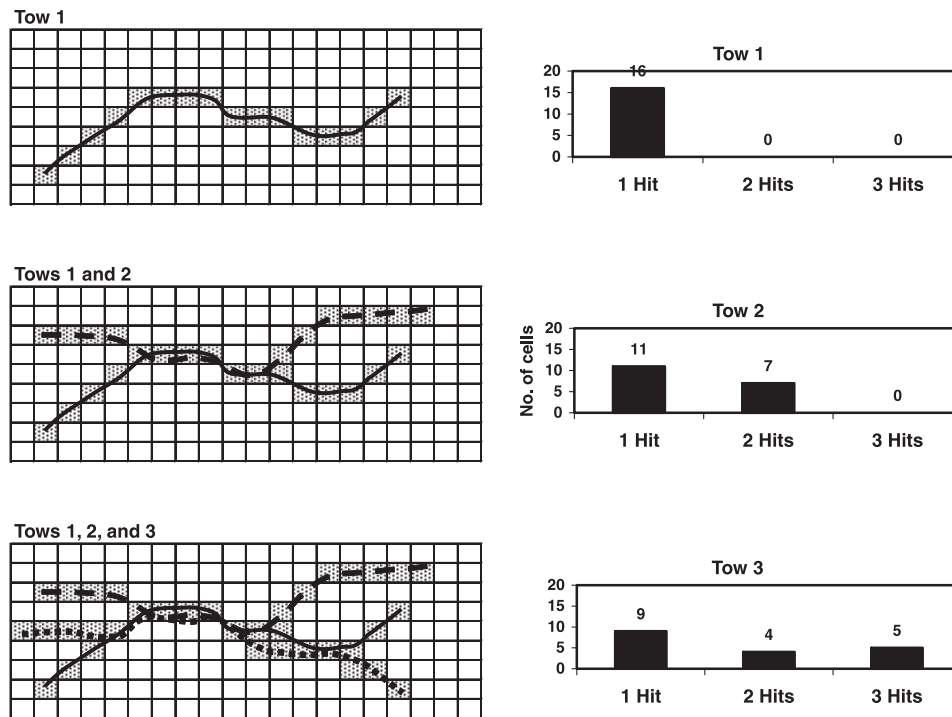
When applying the model, the choice of cell width is an important practical decision related to the accuracy and precision of gear location and gear size. The parameter  $\gamma$  would be 1.0 in an ideal situation with perfect information on the location of the sampling device, a tow width equal to cell width, and a tow path restricted to one and only one cell per unit time. In practice, these conditions are violated to varying degrees. This can be dealt with in a model by selecting a cell width that is commensurate with the imprecision of data on location of the sampling device. For instance, if the location  $\{x, y\}$  of the sampling device is known to within some

**Table 1.** Expected values of density, number (or abundance), catch, and cumulative catch in a hypothetical depletion experiment in one cell, with complete mixing within the cell after each tow.

Dredge pass ( $i$ )	Density ( $D_i$ )	Number ( $N_i$ )	Catch ( $i - 1$ to $i$ ) = $C_i$	Cumulative catch ( $T_i$ )
0	$D_0 = N_0/A$	$N_0$	—	—
1	$D_1 = N_1/A$ $= (N_0/A)(1 - e(a/A))$	$N_1 = N_0 - C_1$ $= N_0 - e(a/A)N_0$ $= N_0(1 - e(a/A))$	$C_1 = eaD_0$ $= e(a/A)N_0$	$T_1 = 0$
2	$D_2 = N_2/A$ $= (N_0/A)(1 - e(a/A))^2$ $= D_0(1 - e(a/A))^2$	$N_2 = N_1 - C_2$ $= N_0(1 - e(a/A)) - e(a/A)N_0(1 - e(a/A))$ $= N_0(1 - e(a/A))(1 - e(a/A))$ $= N_0(1 - e(a/A))^2$	$C_2 = e(a/A)N_1$ $= e(a/A)N_0(1 - e(a/A))$	$T_2 = C_1$ $= e(a/A)N_0$
3	$D_3 = N_3/A$ $= (N_0/A)(1 - e(a/A))^3$ $= D_0(1 - e(a/A))^3$	$N_3 = N_2 - C_3$ $= N_0(1 - e(a/A))^2 - e(a/A)N_0(1 - e(a/A))^2$ $= N_0(1 - e(a/A))^2(1 - e(a/A))$ $= N_0(1 - e(a/A))^3$	$C_3 = e(a/A)N_2$ $= e(a/A)N_0(1 - e(a/A))^2$	$T_3 = C_2 + C_1$ $= e(a/A)N_0 + e(a/A)N_0(1 - e(a/A))$ $= e(a/A)N_0(1 + 1 - e(a/A))$ $= e(a/A)N_0(2 - e(a/A))$

**Note:** The overall area is denoted as  $A$  and the area swept by an individual tow is denoted as  $a$ . Efficiency,  $e$ , is the probability of capture given encounter.

**Fig. 2.** Diagram of depletion experiment with multiple passes over a spatially distributed population. Grids in the left column represent example tow paths; histograms in the right column represent the number of cells that are “hit” one or more times in each tow.



error level  $\delta$ , then the size of the individual cell within a tow path can have an area proportional to the width of the sampling device  $\pm \delta$ .

### Adding “indirect” effects to the model

“Indirect” effects in depletion experiments occur when the sampling process alters the catchability and availability of some individuals to the sampling gear during the experiment. For example, indirect effects may occur if the zone of influence of a clam dredge, used in a depletion experiment, is greater than the width of the dredge or if the availability of clams changes because of the dredge’s effects on the bottom. Clams could be blown out of the area or buried, without being caught by the dredge (Meyer et al. 1981; Murawski and Serchuk 1989a).

With these types of indirect effects, the population available for capture on subsequent passes will be less than that expected based on eq. 4. Alternatively, if buried clams become more exposed to the dredge with each tow, then the reverse would be true. To deal with this general problem, we allow the parameter  $\gamma$  to take on additional meaning. We now use it to represent not only the size of the sampling device relative to cell size, but also the device’s indirect effects on the probability of capture:

$$(6) \quad \gamma = (w_{\text{dredge}}/\Delta x) + \varepsilon$$

where  $w_{\text{dredge}}$  is the width of dredge,  $\Delta x$  is the width of cell, and  $\varepsilon$  is a factor related to indirect effects. When there are no indirect effects,  $\gamma$  equals its nominal value (i.e., the ratio of dredge width to cell width).  $\gamma$  will be greater than the nominal value if animals become less available to the sampling gear with repeated passes over the same cell, or if they are lost be-

fore they can be counted in the catch. Conversely,  $\gamma$  will be less than its nominal value if animals become more available, or new animals become vulnerable to the sampling gear, with repeated passes. If indirect effects exist, it is necessary to estimate  $\gamma$  in a mathematical model, preferably utilizing external empirical information.

### Parameter estimation from the NB distribution

Standard approaches for estimating NB parameters do not apply here because in most depletion experiments tows vary in length. Bissell (1972) showed how to apply the NB model to counts based on varying element sizes, and we applied his results to depletion experiments by writing the tow area as a function of the area swept in tow  $i$ ,  $e$ ,  $\gamma$ , and the pattern of overlap with other tows. We define this as the “effective” area,  $a_i^*$ , of each tow:

$$(7) \quad a_i^* = ea_i \sum_{j=1}^i f_{i,j} (1 - e\gamma)^{j-1}$$

Effective area represents the area sampled after adjusting it downward for cells in the tow path that were sampled a variable number of times during previous tows, which reduces the number of animals available for capture. Our formulation of the NB model is similar to that developed by Power and Moser (1999), who parameterized a model for trawl catches in terms of the volume of water filtered by the  $i$ th tow. Our definition of  $a_i^*$  differs in that it depends on both the area swept by the current tow and all previous tows. In effect, this definition normalizes the area swept in any given tow

with respect to the locations and areas swept by all previous tows.

The NB distribution for catch can be expressed as a function of  $D_0$ ,  $K$ , and  $a_i^*$ :

$$(8) \quad \Pr(C = C_i | D_0, K, a_i^*) = \left( \frac{K}{D_0 a_i^* + K} \right)^k \left( \frac{D_0 a_i^*}{D_0 a_i^* + K} \right)^{C_i} \times \prod_{j=1}^{C_i} \left( \frac{K + j - 1}{j} \right)$$

The log-likelihood function for the parameters  $K$ ,  $D_0$ ,  $e$ , and  $\gamma$  given  $C_i$  and  $a_i$  is

$$(9) \quad \begin{aligned} \text{LL}(K, D_0, e, \gamma | C_i, a_i) = & K \sum_{i=1}^I (\log(K) - \log(D_0 a_i^* + K)) \\ & + \sum_{i=1}^I C_i (\log(D_0 a_i^*) - \log(D_0 a_i^* + K)) \\ & + \sum_{i=1}^I \sum_{j=1}^{C_i} \log(K + j - 1) - \sum_{i=1}^I C_i! \end{aligned}$$

Note that in this formulation, the likelihood function for successive probability density functions of catch are linked by the  $a_i^*$  (eq. 7). This dependency between successive terms in our formulation of the likelihood function for the NB distribution is analogous to the multinomial distribution (used in a standard Leslie–Davis model) obtained from a sequence of linked binomial distributions (Gould et al. 1997, p. 900).

### Profile likelihood confidence intervals

Profile likelihood methods (Venzone and Moolgavkar 1988; Hirst 1994) can be used to estimate approximate confidence intervals for single parameters and confidence regions for two parameters. If  $\theta^* = \{D_0, e, K, \gamma\}$  represents the vector of parameters that maximizes the negative  $\text{LL}(D_0, e, K, \gamma | C_i, a_i)$ , then the profile likelihood for any parameter  $\theta_k$  may be obtained by finding the roots of

$$(10) \quad \text{Sup}[\text{LL}(\theta_k, \theta_{-k}^*)] = \text{LL}(\theta_{-k}^*) + \frac{\chi_{1,\alpha}^2}{2}$$

where  $\theta_{-k}^*$  denotes the parameter vector with all parameters except  $\theta_k$  equal to their maximum likelihood estimates, Sup is the supremum function (Mood et al. 1974), and  $\chi^2$  is the chi square value for a selected  $\alpha$  with 1 df.

Confidence intervals for catch are calculated in the new model by solving for  $C_{\min}$  and  $C_{\max}$  in the following equation:

$$(11) \quad 1 - \alpha = \text{Prob}(C_{\min} < C(a_i^*) < C_{\max})$$

$$= \sum_{C_{\min}}^{C_{\max}} \text{NB}(C_i | a_i, \theta^*)$$

In the new model, the  $G$  test, following White and Bennetts (1996), measures goodness of fit of observed catches to predicted catches.

### Application to an Atlantic surfclam depletion experiment

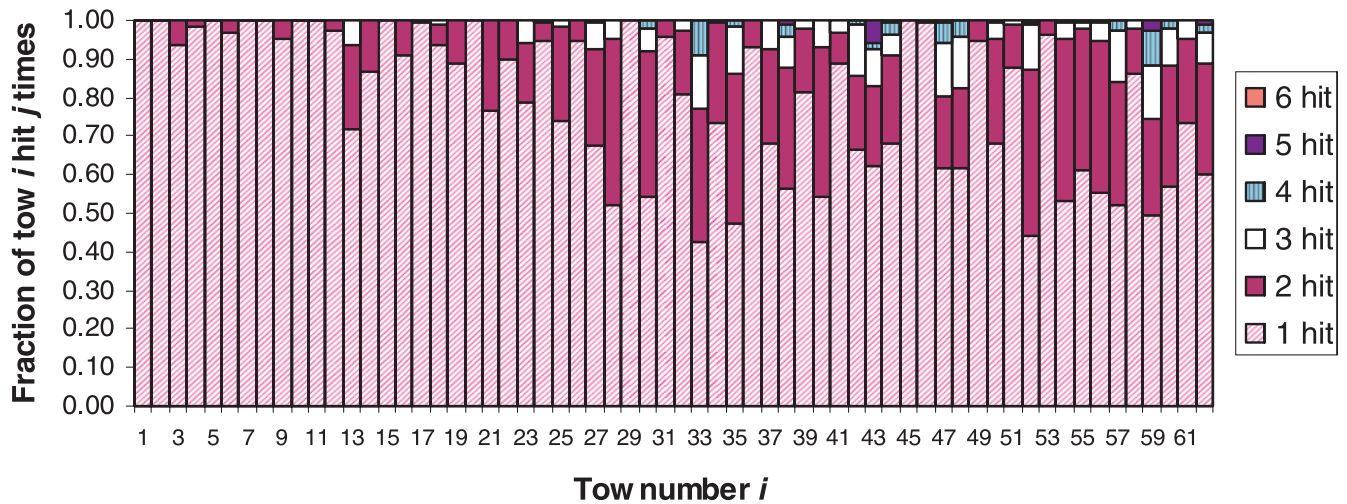
The Atlantic surfclam has been harvested commercially along the east coast of the USA for over 40 years, and it is the basis of a multimillion-dollar fishery (Murawski and Serchuk 1989b; Weinberg 1999; Weinberg et al. 2002a). The National Marine Fisheries Service has carried out fishery-independent surveys of this species with the NOAA R/V *Delaware II* (48 m in length) using a 1.52 m wide, hydraulic clam dredge. The dredge has a submersible pump and weighs 3.2 tonnes. Estimates of dredge efficiency from experiments have been used to convert survey estimates of catch per tow to estimates of total abundance (NEFSC 1998, 2003, 2004). We analyze one depletion experiment here to illustrate the new model and to compare it with the Leslie and Davis (1939) and Gould and Pollock (1997) models. This experiment was conducted off Atlantic City, New Jersey, USA (39°17.64'N latitude, 73°51.55'W longitude) between 5 June 1997 and 11 June 1997 in 34 m of water. The bottom was sand and gravel, the typical substratum for surfclams. Sixty-two tows were made over the same approximate location in an attempt to deplete the area of surfclams. The number of surfclams captured by the dredge in each tow was recorded.

The tow path of the dredge was assumed to match the ship's position, which was measured at 1-s intervals with a differential global positioning system (GPS). Each tow in this experiment was made with a 2:1 scope (tow line length to bottom depth) at 1.5 knots for 2 min, not counting the time that it took to set out and recover the dredge. The average distance between measurements of ship position was 1.25 m. An inclinometer, mounted on the dredge, electronically recorded the dredge angle and allowed us to estimate when the dredge was in contact with the bottom and sampling (Weinberg et al. 2002b).

To apply the model to an actual experiment, it is necessary to estimate the fractional overlap values  $f_{i,j}$  for each tow (eq. 4). The procedure for converting a set of tow-specific coordinates into a set of proportions involves constructing a grid of cells for the experimental area, overlaying the tow tracks over the grid, and computing the number of times that each cell had been previously sampled through the  $i$ th tow. The fraction of the swept area for tow  $i$  that is hit  $j$  times is computed as the ratio of the number of cells hit  $j$  times divided by the total number of cells within tow  $i$ . By definition,  $j \leq i$ . These concepts are illustrated in Fig. 2 for a simplified example. The data matrix used for estimation of parameters in eq. 8 consists of the total catch per tow  $C_i$  and the estimated fraction of the tow  $i$  hit  $j$  times (i.e.,  $f_{i,j}$ ).

Programs to preprocess position data, obtain maximum likelihood estimates, and evaluate goodness of fit were written in FORTRAN. International Mathematics and Statistics Library (IMSL) routines were used for optimization (eq. 9) and root finding (eq. 10). Optimization used Nelder and Mead's (1965) Simplex method, as described in Press et al. (1992). Confidence intervals (eq. 11) were found by evaluating the cumulative distribution function for values of  $a_i$  and  $f_{i,j}$ . After convergence, the model was restarted nine times, with different sets of initial parameter values, to determine if parameter estimates were stable.

**Fig. 3.** The area of each tow in the surfclam (*Spisula solidissima*) experiment is decomposed into the fraction that, at the conclusion of the tow, has been sampled  $j$  ( $j = 1, 2, \dots, 6$ ) times. Each column represents a tow. Elements within columns sum to one.



**Table 2.** Results (point estimates and 95% confidence intervals) from depletion models fit to data from a surfclam (*Spisula solidissima*) experiment.

Model	Dredge efficiency	Clam density (number·m <sup>-2</sup> )
Leslie–Davis (linear regression)	0.552 (0.372–0.731)	0.990 (0.872–1.109)
Gould and Pollock (MLE)	0.535 (0.497–0.573)	1.012 (0.969–1.066)
New model (3.0 × 3.0 m cell size)	0.645 (0.461–0.816)	0.775 (0.646–1.001)
New model (1.5 × 1.5 m cell size)	0.673 (0.557–0.674)	0.700 (0.646–0.818)

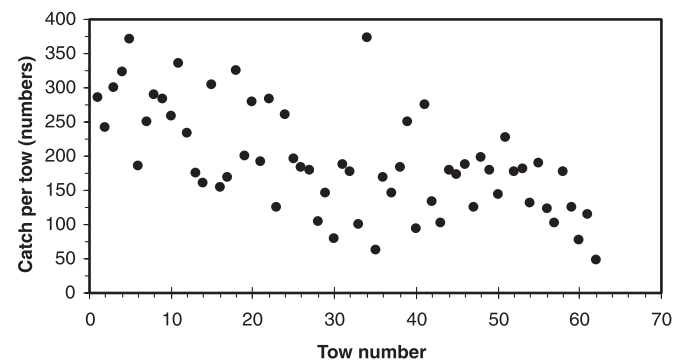
**Note:** The Leslie–Davis interval is a standard confidence interval from a linear regression in which errors are assumed to be normally distributed. Other intervals are from profile likelihoods for the multinomial model (MLE (maximum likelihood estimation); Gould and Pollock 1997) and the new, negative binomial model presented in this paper.

This depletion experiment sampled a rectangular area approximately 500 m × 175 m (NEFSC 1998). We used a 3.05 × 3.05 m cell size because of uncertainty in the exact position of the dredge in the sampling grid and because successive ship position measurements were, on average, 1.22 m apart.

Following eqs. 4 to 5, we computed the hit frequency matrix (Fig. 3). For the first 12 tows, carried out at the beginning of the experiment, 90%–100% of their areas were sampled for the first time. As the experiment progressed, tows tended to have a greater fraction of their total area sampled previously. The tows in this experiment were dispersed over a relatively large area, so even the final tows were still sampling new ground for approximately 50%–60% of their paths. For the entire experiment, the maximum number of times that any cell was contacted was six. The observed catch ranged from about 50 to 400 individuals per tow, and catch per tow declined over the course of the experiment (Fig. 4).

Parameter estimates were 0.645 for dredge efficiency and 0.775 clams·m<sup>-2</sup> for density (Table 2). The 95% confidence interval for efficiency ranged from 0.46 to 0.82, whereas the interval for density ranged from 0.65 to 1.00 surfclams·m<sup>-2</sup> (Table 2). The elliptical joint 95% confidence region for efficiency and density, based on profile likelihood, demonstrated the negative correlation between these parameters (Fig. 5a), expected in depletion studies. For this experiment, the confidence regions for  $\gamma$  and efficiency (Fig. 5b) and  $\gamma$  and density

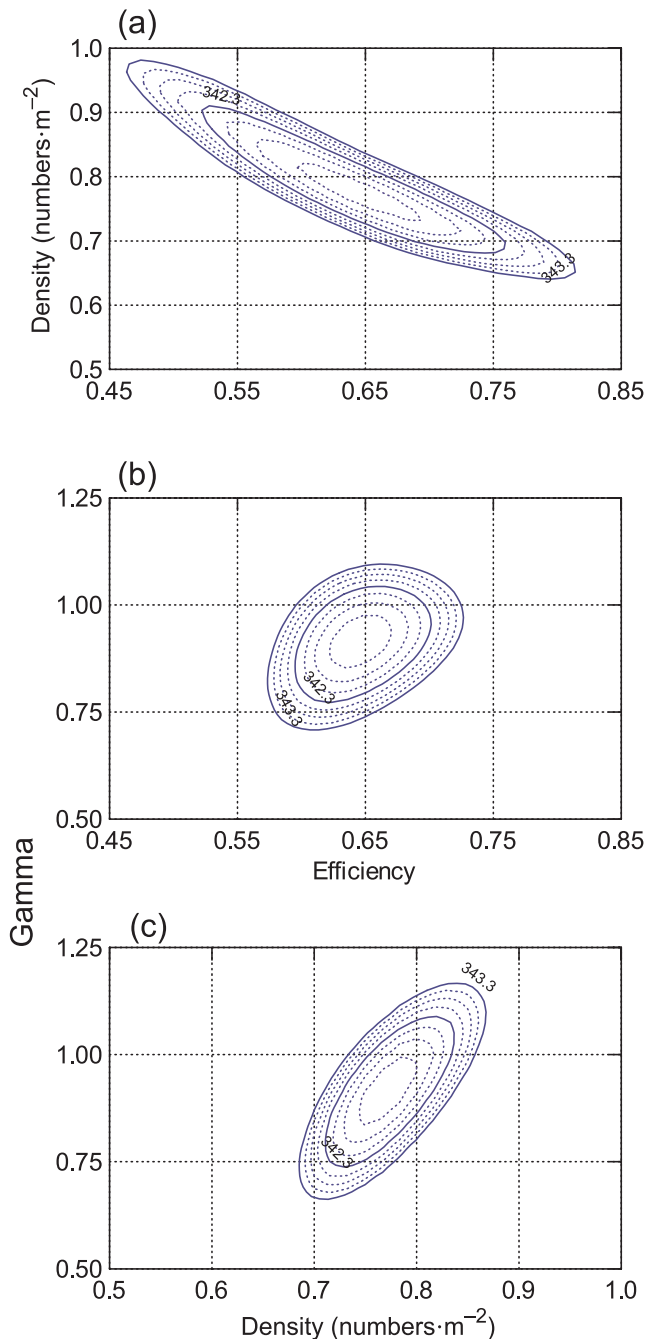
**Fig. 4.** Number of surfclams (*Spisula solidissima*), by tow, captured and counted during the depletion experiment.



(Fig. 5c) were relatively small. Estimates of  $\gamma$  and density were positively correlated, whereas the joint confidence region for  $\gamma$  and efficiency suggested that estimates of these parameters were nearly independent. Other applications of our model suggest that this may not be true in all cases.

There was a positive relationship between observed catch per tow and effective area sampled (eq. 7) per tow (Fig. 6). This relationship occurred because catch per tow was affected not only by the density of clams at the start of the experiment and tow length, but also by catch history and spatial aspects of sampling. Residuals for observed and predicted catches (Fig. 7) and comparison of observed and pre-

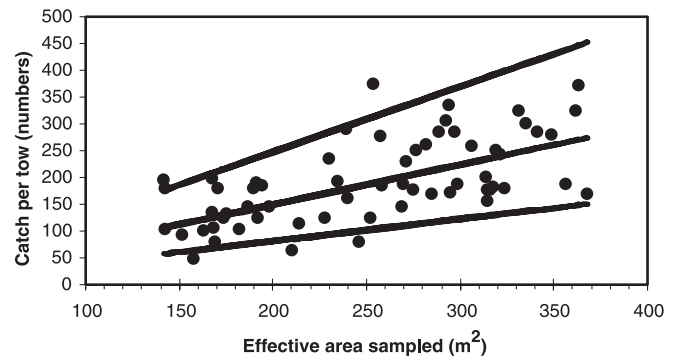
**Fig. 5.** Profile likelihood confidence regions for (a) surfclam (*Spisula solidissima*) density (number·m<sup>-2</sup>) and capture efficiency, (b) gamma and capture efficiency, and (c) gamma and surfclam density (number·m<sup>-2</sup>) in the surfclam experiment. Outermost ellipse is a 95% joint confidence interval.



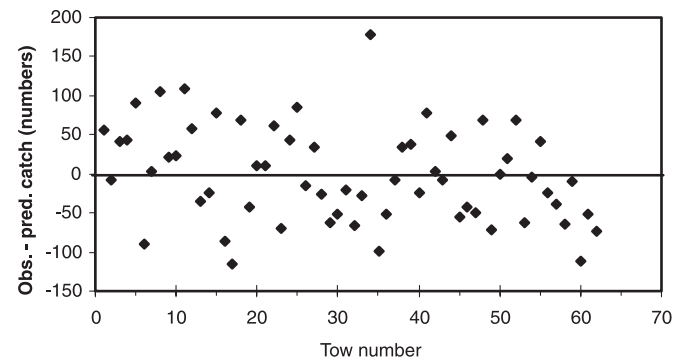
dicted frequency distributions for catch per tow (Fig. 8) suggested good model fit. Based on a  $G$  test, there was not a significant difference between these frequency distributions ( $G = 13.51$ ,  $df = 10$ ,  $p = 0.197$ ; Fig. 8).

$\gamma$  was estimated to be 0.918, which is greater than the nominal (i.e., expected) value based only on the ratio of dredge width to cell width (0.5). This suggested that indirect losses of clams took place during this experiment. Because  $\gamma$  is a dimensionless ratio, it is difficult to grasp the meaning

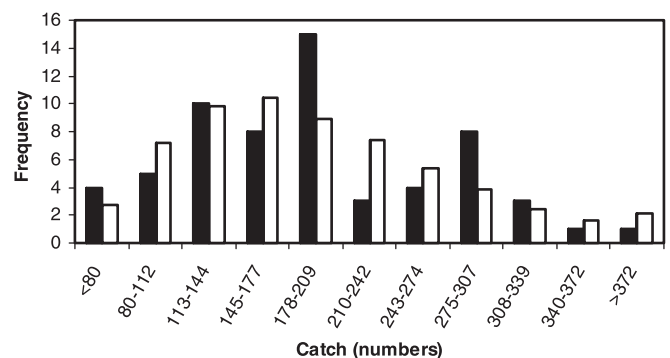
**Fig. 6.** Observed (●) and predicted (lines) surfclam (*Spisula solidissima*) catch per tow as a function of effective area sampled. Predicted values are from a parametric percentile method, computed with eq. 10. They represent the median and 95% confidence interval.



**Fig. 7.** Plot of residuals (observed (Obs.) – predicted (pred.) surfclam (*Spisula solidissima*) catch) vs. tow number.



**Fig. 8.** Observed (open bars) and predicted (solid bars) frequency distributions for surfclam (*Spisula solidissima*) catch per tow. Predicted catch is based on the negative binomial model.



of a change in  $\gamma$  from 0.5 to 0.918. To clarify this, we did a sensitivity analysis to measure the impact on the predicted catch of changing  $\gamma$  (following eq. 4). In the sensitivity analysis,  $\gamma$  was varied between 0.4 and 1.2, while density, efficiency, and the dispersion parameter  $K$  were held at their optimal values. Lowering  $\gamma$  from 0.918 to 0.4 caused the predicted average catch per tow to increase by +10%. Raising  $\gamma$  from 0.918 to 1.2 decreased the predicted average catch per tow by -6%. Reducing  $\gamma$  below its optimal solution of 0.918 simulated reducing the number of clams lost due to

indirect factors and raised the predicted catch in the dredge. Conversely, raising  $\gamma$  above 0.918 simulated even greater loss of clams due to indirect effects and lowered the predicted catch in the dredge.

We pointed out that  $\gamma$  may be difficult to determine. Because of this, we examined the sensitivity of efficiency and density to the assumed value of  $\gamma$ . Fixed  $\gamma$  values between 0.5 and 1.0 were used to the new model, assuming a  $3.05 \text{ m} \times 3.05 \text{ m}$  cell size, while the solutions for the other parameters were not constrained. Estimates of dredge efficiency were negatively correlated with  $\gamma$ , whereas density was positively correlated with  $\gamma$ . As  $\gamma$  increased from 0.5 to 1.0, dredge efficiency estimates decreased from about 0.9 to about 0.6, whereas density increased from about 0.5 to  $0.8 \text{ surfclams} \cdot \text{m}^{-2}$  (Fig. 9).

Given the quality of spatial information for this experiment, a cell size of  $3.05 \text{ m} \times 3.05 \text{ m}$  was judged appropriate. In one model run, we explored the sensitivity of parameter estimates to cell size using a smaller cell size of  $1.52 \text{ m} \times 1.52 \text{ m}$ . Point estimates for density and efficiency did not change substantially from those in the run with  $3.05 \text{ m} \times 3.05 \text{ m}$  cells, but reducing the cell size caused the confidence intervals to be smaller (Table 2). Thus, using a cell size that is too small does not appear to cause much bias in parameter estimates, but it causes underestimation of variances of the parameters.

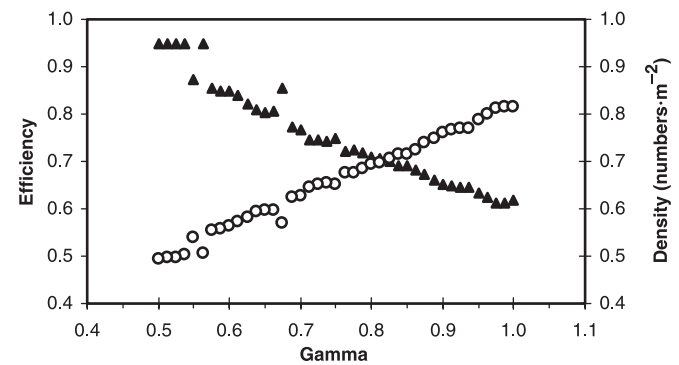
### Comparison of results with other depletion models

Point estimates for capture efficiency ranged from 0.54 in the Gould and Pollock model to 0.67 in the present model, with a  $1.52 \text{ m} \times 1.52 \text{ m}$  cell size (Table 2). Point estimates from the Leslie–Davis model and the Gould and Pollock model were similar to each other, as were the estimates from the two runs of the spatial model using different cell sizes. For dredge efficiency, the narrowest confidence interval (0.08) was associated with the Gould and Pollock model. The spatial model with a  $1.52 \text{ m} \times 1.52 \text{ m}$  cell size produced a slightly wider interval (0.12). The widest confidence interval (0.36) was associated with the Leslie–Davis model and the present model, in which we used a  $3.05 \text{ m} \times 3.05 \text{ m}$  cell size.

### Discussion

Traditional models for analyzing depletion experiments do not take into account important factors such as the history of catches from individual cells, the inability of sessile organisms to redistribute themselves between tows, indirect effects of sampling gear on availability and probability of capture of organisms, and differences in sampling intensity between locations. The model presented here considers these factors. The new model is appropriate to use when accurate information is available on the location of each sample and the overlap between samples, when organisms do not redistribute themselves quickly, when indirect effects occur, and (or) when it is necessary to sample with large dredges, the positions of which are hard to control. In situations when information about the location of each sample is not available,

**Fig. 9.** Gamma was varied from 0.5 to 1.0 to determine its effect on two other parameters in the new model, clam (*Spisula solidissima*) density ( $\circ$ ) and capture efficiency ( $\blacktriangle$ ).



the model reduces to a simpler model comparable to model 2 of Schnute (1983).

Implementing the new spatial model and collecting the necessary data require technologies such as GPS and geographical information system (GIS). GPS is used in the field to position the ship and record instantaneous location during each tow, and GIS is used in data analysis to visualize tow paths and compute degree of overlap among tows. Improvements in our ability to locate the dredge in two-dimensional space will let us reduce cell size and increase the precision of the overlap (“hits”) indices. The effect of imprecise location information is an important topic for future research.

The new model allows for analyses of depletion experiments that vary in total area and in which tows vary in length. To our knowledge, this is the first model for analysis of depletion experiments that utilizes the NB distribution, an appropriate statistical model for overdispersed catches of organisms in nature (Power and Moser 1999). Gould and Pollock (1997) addressed overdispersed catches using quasi-likelihood methods in their analysis of the lobster (*Homarus americanus*) data of Paloheimo (1963). Wang and Loneragan (1996) proposed a more complicated compound distribution wherein the catchability parameter was distributed as a beta random variable. Either approach would be sufficient to address the effects of overdispersion.

Under the usual assumptions of the Leslie–Davis model, the joint distribution of the realized set of catches reduces to a multinomial distribution. The multinomial distribution can be used because (i) the mean and variance of a single tow can be expressed as a function of the probability of capture and the total population at the time of the sample, and (ii) the realization of catch in all previous tows alters the probability density function (pdf) of each catch in the series.

Although the multinomial distribution is a convenient closed-form expression of the joint distribution, other approaches could be used to model the salient features of a depletion experiment. Any model that is used must describe the capture process and link the distributions between successive tows. Explicit linkage of the pdfs is evident in earlier literature in which the multinomial distribution for removal experiments was called a “chain binomial” (Pielou 1977). As another illustration, Wang and Loneragan (1996) characterized the joint pdf as a beta-binomial distribution.

In our formulation of the depletion experiment, we chose to explicitly model the capture process with a NB model allowing a transition from random to overdispersed catches. The magnitude of overdispersion is indexed by  $K$ : when  $K$  is large the model converges to a Poisson distribution, which can be approximated by a binomial distribution (Mood et al. 1974). Our model also preserves the explicit dependency in the likelihood function such that each catch is dependent on previous tows. However, this dependency is not based on order as in the standard depletion model. Instead, it depends on the degree of spatial overlap of the current catch with all previous catches, as represented by their respective tow paths. The dependency of terms in the joint density function for catches in a depletion experiment for sessile organisms is handled through the computed measures of spatial overlap  $f_{i,j}$  and the spatially explicit cell- or patch-based formulation in which each tow path hits a linked set of cells. The resulting joint distribution of catches may have a closed-form distribution, but we have not investigated this.

Differences in parameter estimates between the new model and traditional depletion models are caused by at least two factors. First, there is no explicit treatment of degree of tow overlap in the Leslie–Davis model; therefore, one might incorrectly interpret a high catch resulting from sampling new ground late in a depletion experiment as a low dredge efficiency. Second, indirect effects are not included in the Leslie–Davis model, so it might overestimate dredge efficiency by incorrectly attributing a low catch per tow to efficiency rather than to indirect effects of the gear in cases when it lowers the catchability of animals. These two factors bias the efficiency estimate in opposing directions and could even cancel each other out. Because the new model can realistically incorporate information on tows paths and indirect effects, it might yield more accurate estimates of the parameters and their variances. Thus far, the new model has been applied, for stock assessment, to data from numerous depletion experiments involving clams and scallops from the US Atlantic coast (NEFSC 2001, 2003, 2004).

When applied to the surfclam data, the Gould and Pollock model produced the smallest confidence intervals for both dredge efficiency and clam density. However, low variance may have resulted from model misspecification because the model did not consider the spatial distribution of clams. Wang and Loneragan (1996) showed that uncertainties in estimates of  $N$  and  $q$  were underestimated by standard approaches, which did not address overdispersion of organisms. They attempted to incorporate the spatial pattern of organisms by treating the catchability parameter  $q$  in their model as a random number from a beta distribution. Earlier, Crittenden (1983) attempted to model the capture process by explicitly incorporating an aggregation factor into the Leslie–Davis model. Variations in catchability have also been modeled as explicit functions of environmental parameters (Yamakawa et al. 1994), competing species (Polovina 1986), and independent signs of animal activity (Routledge 1989). We have modeled catchability as an explicit function of the spatial pattern of overlap among tows.

### Gamma, cell size, and the catchability parameter

In practice, direct and indirect information about the behavior of the dredge, the animals, and their interactions

could be used in a Bayesian approach to specify a likely range of values for  $\gamma$ . For the experiment considered here, empirical studies (Meyer et al. 1981; Murawski and Serchuk 1989a) indicated that the influence of the dredge on clams could extend half a dredge width beyond its nominal value. A lower bound would be one dredge width. Using a  $\gamma$  value greater than the ratio of the dredge width to cell width would imply that the expected population size within a cell that is available to the dredge on subsequent passes has been reduced beyond that explained by observed catches.

The  $\gamma$  parameter is also related to the selection of the appropriate cell size for applying the spatial model. At the extreme, as the cell size in the model increases, approaching the size of the area of the entire multiple-tow experiment, the new spatial model converges to the nonspatial Leslie–Davis model. Choice of cell size must be scaled to the degree of uncertainty about the position of the sampling gear and the tenability of the assumption of equal catchability of animals between samples, at the level of the cell. In the surfclam experiment, it was possible to run the spatial model with a cell size equal to or less than one dredge width. In that case, variances of parameters would be underestimated because the true position of the dredge is not known with such accuracy. This explains why the confidence intervals were much smaller when the new model was run with a 1.52 m  $\times$  1.52 m cell size, compared with the more appropriate 3.05 m  $\times$  3.05 m cell size. The cell size of 3.05 m  $\times$  3.05 m was more appropriate given the distance between successive ship positions, the dredge width, and uncertainty about dredge location. Using a cell size greater than the width of the dredge reflected the positional uncertainty of the dredge appropriately, but using a larger cell made the assumption about equal catchability of animals within cells between tows less tenable. Thus, there is a trade-off between cell size and satisfying the equal-catchability assumption. This assumption is more likely to be satisfied if a sensor could be used to track the location of the dredge directly (e.g., Takeda et al. 1995), making it appropriate to choose a smaller cell size for modeling.

Through the  $\gamma$  parameter, we presented one formulation of the capture process in which indirect losses of individuals may occur. Schnute (1983) considered other hypotheses, which could be included in our model by modifying eq. 4. Schnute considered the situation in which catchability declined with successive samples. For example, the efficiency of the first pass over an area can differ from that in subsequent samples, leading to a model with two efficiency parameters (Schnute 1983, model 2, p. 2155). A similar concept has been incorporated in models for electroshocking of fish in streams (Riley and Fausch 1992). In wildlife studies, the  $M_h$  and  $M_t$  models of Otis et al. (1978) allow for changes in catchability among animals and among recapture periods, respectively. Kendall and Bjorkland (2001) addressed the problem of temporary emigration of sea turtles (*Eretmochelys imbricata*) from the study area by allowing the probability of detection in a time period to vary. Their model was able to obtain unbiased estimates of survival and breeding probabilities.

Our model does not explicitly model variations in initial density over the area of the depletion experiment. Such variations might arise from habitat discontinuities (e.g., discrete

beds of scallops; Caddy 1975). Nevertheless, the  $K$  parameter in the NB model provides some indirect information on the spatial heterogeneity (Pielou 1977; White and Bennetts 1996). The biases inherent in a nonspatial treatment of depletion experiments for sessile animals were demonstrated herein. Because the new model considers the spatial pattern of the animals and the tows, it should reduce the potential for these biases. Although many models can be used to describe overdispersion, the NB model has proved useful in many fisheries applications. A formal validation of the new model via extensive simulation experiments will be the subject of a future paper. Preliminary simulations have shown that the model can effectively recover the underlying parameters. In our application of the model to other species (NEFSC 2000b, 2001, 2004), we have found that the  $\gamma$  parameter is not always identifiable. The ability to estimate all four model parameters is related to the overlap pattern of tows within a depletion experiment. Tows that overlap extensively will be more informative about the joint effects of the efficiency and  $\gamma$  parameters.

This paper presents a realistic and flexible model for analyzing depletion experiments to estimate catch efficiency and density of organisms in an area. When combined with population abundance indices from standardized surveys, gear efficiency estimates can play an important role in direct stock size estimation (Vølstad et al. 2000; NEFSC 2003, 2004). Because gear efficiency may vary with habitat (NEFSC 2000a, 2000b), surveys that include multiple habitats may require multiple depletion experiments. From a statistical perspective, the benefit of measuring catch efficiency in several habitats may surpass the value of increasing the number of samples (tows) in a survey (Vølstad et al. 2000). Our conclusions are consistent with those of Schnute (1983), who advanced the notion that parametric descriptions of changing catchability were important aspects of depletion experiments in fisheries.

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